Comparative Observations on Reproduction, Spawning, and Early Veligers of Three Common Subtidal Mesogastropods from North Central Chile

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Abstract. The egg masses and hatched veliger larvae of three mesogastropod species from La Herradura Bay, Coquimbo, Chile are described, including: *Turritella cingulata* Sowerby, 1833, *Sinum cymba* (Menke, 1828), and *Priene* scabrum (King, 1832).

The morphology of the egg masses was similar to the descriptions given for other members of these families. The egg mass of *Turritella cingulata* consisted of a gelatinous matrix mixed with sand, weighing an average of 2.04 g. Egg capsules were embedded in the matrix; they were spherical, translucent, and contained one to 15 embryos. Development lasted 7–8 days at 13.5–14.0°C. The hatched veligers measured 141 μ m in length. The egg mass of *Sinum cymba* was ribbonlike with two sand layers in between which were located spherical, transparent egg capsules. Each capsule contained one embryo. Hatching larvae measured 194 μ m in length. *Priene scabrum* laid on average 129 capsules in each egg mass. The capsules were vasiform in shape, 3.6×6.0 mm in length, and each contained an average of 1466 embryos. The intracapsular period lasted 38 days at 14 ± 0.4°C, and hatched larvae measured 263 μ m in length. All three species had indirect development.

INTRODUCTION

The mesogastropods represent the largest group within the prosobranch mollusks and show the highest diversity in reproductive biology. The majority are dioecious, with internal fertilization by means of copulation. Development of the eggs occurs partially or completely within egg capsules, which are usually deposited in masses closely associated with the substrate in their habitat (Webber, 1977). Many specific characteristics of the reproductive process of prosobranch mollusks allow grouping or identification of individuals to the family, genus, or species level, and allow inference of evolutionary relationships between them (Robertson, 1974; D'Asaro, 1991). Characteristics of egg deposition have been very useful tools in molluscan taxonomy (Giglioli, 1955; Amio, 1955; Ziegelmeier, 1961; Lebour, 1936; Thorson, 1950; D'Asaro, 1970, 1991; Barash & Zenziper, 1980; Gallardo, 1981; Cañete, 1992). Robertson (1974) listed five diagnostic characters useful in these studies: (1) egg deposition; (2) mode of development (hatching stage); (3) morphology of the veliger larva; (4) size at which metamorphosis occurs, and (5) size of the egg.

Within the mesogastropods, ovipositional forms include tubular or vasiform capsules, flat helical belts, or amorphous gelatinous masses (Hyman, 1967; Robertson, 1974). Occurrence of oviposition provides a direct indication of sexual maturity in individuals, such that these organisms may be easily recognized in the environment without the need to sacrifice specimens for histological observation. These aspects, as well as the knowledge of their development and type of larvae, are useful in studies of biodiversity, evolutionary relationships, and ecology, as well as in the management of species valued as food for humans (Thorson, 1950; Robertson, 1974; Barkati & Ahmed, 1983; Cañete, 1992).

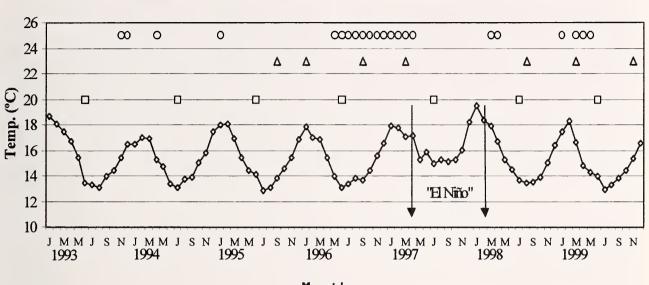
The present study describes the egg deposition, capsule, number of embryos per capsule, and morphology of hatched veliger larvae of three mesogastropod species in La Herradura Bay, Chile, including *Turritella cingulata* Sowerby, 1833 (Turritellidae), *Sinum cymba* (Menke, 1828) (Naticidae), and *Priene scabrum* (King, 1832) (Cymatiidae).

METHODS AND MATERIALS

Between April 1996 and March 1997 observations were carried out weekly by scuba diving in order to determine spawning seasons and reproductive sites for obtaining egg masses. In addition, sporadic observations were added about every 45 days between 1993 and 1999. The three snail species studied were: *Turritella cingulata, Sinum cymba*, and *Priene scabrum* in benthic areas on La Herradura Bay, Coquimbo (29°58'S, 71°21'W). Spawning was observed in reproductive groupings of *Turritella cingulata* and *Priene scabrum* and as individual spawning

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→ Temp. □ P.scabrum △ T.cingulata ○ S.cymba

Months

Figure 1. Observations of egg deposition of three species of mesogastropods in relationship to temperatures of La Herradura Bay. Observations of the three species were done every 7 days from April 1996 to March 1997. During the other years, observations were made every 45 days. For *Sinum cymba*, occasions are indicated only in which egg masses were collected and transported to the laboratory. (El Niño = phenomenon of "El Niño" in La Herradura Bay lasted from April 1997 to March 1998).

of *Sinum cymba*. Temperatures in the bay were measured weekly; average monthly values are shown in Figure 1.

Egg masses were collected by hand from sand or shelly bottoms in diverse areas of the bay and maintained in our laboratory in 2 L aquaria with filtered seawater (1 μ m) for observation and laboratory preparation. Observations and measurements were made under a 20× stereoscopic microscope on the number, form, and sizes of capsules per deposition, as well as the number of embryos and their development stage.

Since egg masses of *T. cingulata* were soft and irregular, they were fixed in 2% glutaraldehyde and were weighed and measured volumetrically using a mL graduated cylinder calibrated to 0.1 mL. From 30 randomly collected depositions, a subsample was weighted and measured, and then the number of capsules within the sample was counted using a stereoscopic microscope. Using this value, the total number of capsules per spawning was estimated. To determine the number of embryos per capsule, from 42 masses, 1771 capsules were counted.

Length of the egg masses of *S. cymba* was measured along the median line of the deposit to the nearest mm; width was measured at the midway point. Pieces of the straplike egg mass measuring 1 cm² were cut from the lower median border for enumeration of capsules contained per unit area. Ten pieces in vertical transection were observed to count the number of egg spaces. Stages of embryos contained in the egg mass were determined by observing the lower part of the egg mass from areas excised from initially deposited and terminally deposited extremes from 18 spawnings.

Size of capsules from *Priene scabrunt* was estimated with a micrometer-equipped stereoscopic microscope, measuring 10 capsules randomly selected from 11 spawnings. Embryo counts were obtained by using all capsular contents from 52 capsules. Eggs and veliger larvae were observed and measured using light microscopy with an ocular micrometer. Maximum length of the protoconch was that measured from the border of the aperture to the extreme base of the protoconch, in lateral view.

Spawnings were maintained in 1 L glass beakers with 1 μ m filtered seawater which was changed daily, at which time the temperature was measured.

Protoconchs of hatched larvae were washed with a 1: 9 seawater dilution of commercial hypochlorite, air dried, and then gold-coated for SEM observation using JFC-1100 Ion Sputter equipment. Samples were observed and photographed with a JEOL-JSM-T300 scanning electron microscope.

RESULTS

Turritella cingulata

Groups of these snails were observed in the process of spawning in the bay in patches at 3–5 m depth on fine sand and coarse shelly sand areas. Spawnings were observed during the spring (September 1995, 1996; August 1998; and November 1999) and the summer (January

1996; March 1997 and 1999) with egg deposition restricted within the month cited. The ambient seawater temperature ranged from 13.4–13.9°C (spring) to 16.6–17.8°C (summer), respectively. The egg deposition was not observed during September 1997 (spring) when the water temperature was 15.4°C (Figure 1).

The spawn of T. cingulata was composed of a transparent, amorphous gelatinous matrix in which the capsules which contained the embryos were embedded. Recently produced matrix was strongly adhesive, but soon caused it to be covered with particles of sand and other detritus (Figure 2A). The capsules contained in the matrix were spherical, measuring about 352 µm in diameter (SD = 83.2; n = 83) (Figure 2B). Each capsule contained from one to 15 embryos, with most frequent values being two (19% of capsules), three (23% of capsules), and four (18% of capsules) embryos per capsule. Egg masses weighed an average of 2.04 g (SD = 1.06; n = 40), and were about 2.08 mL in volume (SD = 1.02; n = 40). A subsample obtained from 30 spawnings picked randomly showed an average of 11,130 capsules per spawning (SD = 7099; n = 30).

The eggs measured 92 μ m diameter (SD = 8.3, n = 150), were spherical, and opaque white in color. All embryos in the capsules hatched as veliger larvae. Development from the egg to hatching of veligers lasted 7 to 8 days at 13.5–14.0°C. The protoconch of hatched larvae was yellow-brown in color, with an average length of 141 μ m (SD = 10; n = 62). It had a deep initial suture and surface irregularities giving it a rough appearance (Figure 2C). The aperture was circular, weakly tending toward triangular in the dorsal region (Figure 2D). Hatched larvae were bilobed, with non-pigmented velar lobes. Eyespots and tentacles could not be seen under light microscopy. The foot was not pigmented and was triangular in shape with rounded lateral borders, and a thickened central portion heavily covered with cilia (Figure 2E).

Sinun cymba

Egg depositions of this species were frequently found between 8 and 10 m depth on sandy bottoms. Observations made between November 1993 and March 1999 and also from April 1996 to March 1997, suggested that this species carried on reproductive activity throughout the year.

The definition of terms used to characterize the egg

depositions of Sinum cymba follows Giglioli (1955). Egg depositions took the form of a helical belt, with its ends superposed. Due to flexibility of the belt, the length of superposition was variable. All edges of the egg belt were smooth, with the upper margin curved toward the exterior, and shorter than the lower margin, producing an inverted bowl shape. The lateral edges of the belt showed diagonal bends in opposite directions. The leading edge of the belt can be recognized by its extreme upward angle as viewed from outside, lying to the left (Figure 3A). The average length of the belt, measured at the center, was 32.8 cm (SD = 6.2; n = 50), the width was 5.6 cm (SD = 0.6; n = 50), and the thickness was 0.98 cm (SD = 0.43; n = 10). The capsules containing the embryos were spherical and transparent, measuring 178 µm in diameter (SD = 7.3; n = 150). In vertical transection, the belt was composed of two layers of a fibrous matrix interspersed with sand grains. Between the two layers with sand, an indeterminate number of egg capsules were grouped into spaces or cells formed by fibrous septae and sand in the horizontal axis (Figure 3B). On average, 54 egg spaces (SD = 3.8; n = 10) were arranged on a single median plane, and this was continuous from the apical to the basal margin of the belt. Each belt contained about 4015 capsules per cm^2 (SD = 841; n = 10) which are easily separated from the cells. Each capsule contained a single embryo (n = 300).

The average size of the eggs of this species was 126 μ m (SD = 10; n = 62), and they were opaque white in color. The intracapsular development lasted 12 days at 16–18°C. The protoconch of the hatched veliger was brown, with an average length of 194 μ m (SD = 6; n = 33); it was ornamented with granules arranged in longitudinal bands (Figure 3C) and had a semi-circular aperture (Figure 3D). Hatched veliger larvae were planktotrophic, with an unpigmented, bilobed velum. Only the right cephalic tentacle was developed, with a small protuberance at the site of the future left tentacle. Black eyespots were observed at the base of the present and future tentacles. The foot was diamond-shaped with straight sides, and was not pigmented (Figure 3E).

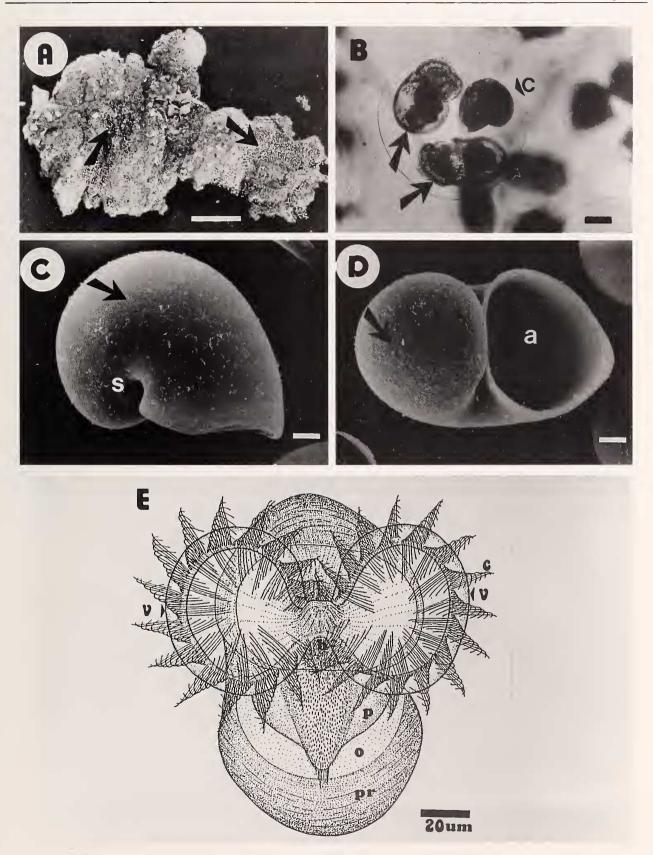
Priene scabrum

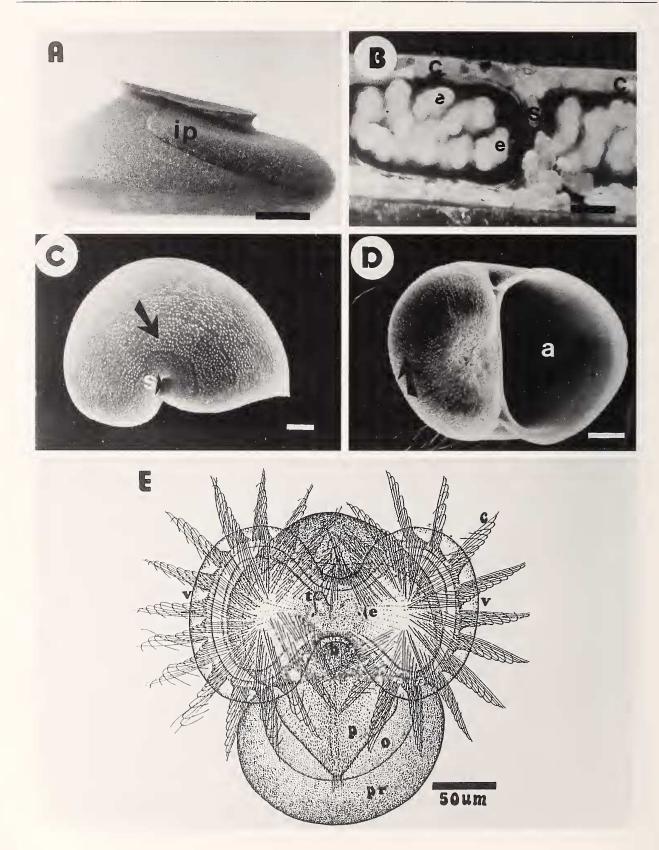
This species reproduced in June and July, based on observations made between 1993 and 1999 (Figure 1). During this period, groups of reproducing adults aggre-

Figure 2. Egg mass and larvae of *Turritella cingulata*. A. The spawn consists of a gelatinous mass mixed with sand, within which are included capsules containing the embryos (arrow indicates some encapsulated embryos). Scale bar = 1 cm. B. Magnified view of part of the egg mass showing capsules with contained embryos. (c = capsule; arrows indicate encapsulated veligers). Scale bar = $60 \ \mu m$. C. Side view of protoconch of recently hatched veliger larvae (s = suture; arrow indicates relief). D. Ventral view of protoconch of recently hatched veliger larva (a = aperture, arrow indicates relief). Scale bar = $15 \ \mu m$. E. Frontal view of recently hatched veliger larva (b = mouth; c = cilia; o = operculum; p = foot; pr = protoconch, v = velar lobes).

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gated at depths of 7–8 m on rocks, piling and other bottom relief, where they deposited their capsules. The spawning coincided with low winter temperatures (approx. 13° C).

Deposits from this species included groups of 129 capsules on average (SD = 46; n = 37) attached to the substrate in circular arrangements (Figure 4A). The capsules were of the vasiform type described by D'Asaro (1991). In transverse section they were oval or semi-triangular. The capsules were transparent, glassy, and rigid (Figure 4B). Capsules were about 6 mm in height (SD = 0.7; n = 110) and 3.5 mm in width (SD = 0.4; n = 110), and each contained an average of 1466 embryos (SD = 628.5; n = 52).

The eggs of P. scabrum were opaque yellow in color, and had an average diameter of 170 μ m (SD = 18.9; n = 60). Hatching took place 38 days after oviposition at a temperature of 14 ± 0.4 °C. The average length of the protoconch of hatched larvae was 263 μ m (SD = 13.7; n = 69; was golden brown, and vitelline material retained within its interior had a yellow tone. The protoconch as visualized by SEM showed aggregations of tubercles in starlike forms (Figure 4C). The aperture was semi-circular, and lateral borders of the aperture were curved toward the exterior (Figure 4D). Hatched veliger larvae were planktotrophic, with an unpigmented, bilobed velum. Two small, dark brown eyespots were visible in the cephalic region, with the right tentacle appearing as a small protuberance with a few apical bristles. The left tentacle was represented by a small blunt swelling. From the ventral view, the foot appeared straight with a triangular projection in the central region (metapodium) projecting past the operculum, having bristles at its posterior end (Figure 4E).

DISCUSSION

Reproductive Cycle

The presence of egg deposits was a good indicator of reproductive cycle in these species. The continuous observations in 1996 and sporadic observations in the other years suggest that *Sinum cymba* reproduces throughout the year, whereas *Priene scabrum* and *Turritella cingulata* showed seasonal reproductive cycles. *P. scabrun* had a well defined spawning season, associated with the months of June and July, which were the coldest months of the year, as verified over 7 years of observations.

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Observations of spawning in T. cingulata over 41/2 years suggested a semi-annual cycle, with reproduction at the beginning of spring and again in summer. However, this species showed significant fluctuations in spawning dates. Beginning with the observations of 1995-1996, spawnings were expected for January of 1997, but were not observed. The spawning of 1997 was displaced to the month of March; in the spring of that year and the summer of 1998, no spawnings were observed. Both in September 1997 and January 1998, a temperature rise of 2°C above the previous 2 years (on the same dates) was observed in La Herradura Bay. This variation was in agreement with the report on the presence of the El Niño phenomenon (Comisión Permanente del Pacífico Sur, 1997, 1998) and may explain the absence of egg masses of T. cingulata, in spite of extensive diving efforts made to observe such egg masses in those months (Figure 1). In 1999 spawnings were again seen in summer and spring, the latter associated with normal temperatures for the season, although these were somewhat higher than those observed in previous years. It is important to consider that the temperature is only one of several factors influencing reproduction in the mollusks (Fretter, 1984). Observations need to be made in future years in order to establish the reproductive cycle of this species with more certainty, and determine if it is as sensitive to temperature as suggested by the results of this study.

Egg Mass and Larvae

The forms of egg deposition, capsules, larvae, and modes of development of the three species presently reviewed were similar to those described for related species from other localities.

Turritella cingulata

Eggs deposited in gelatinous masses are characteristic of the Turritellidae (Hyman, 1967; Webber, 1977). The egg masses of *Turritella gonostoma* (Allmon et al., 1992) are characterized by capsules loosely united to a central membrane which is attached to the substrate by one or two adhesive discs. The egg masses of *T. communis* (Lebour, 1933; Kennedy & Keegan, 1992) have capsules united by a peduncle to a central line. Bandel (1976) described the egg masses of *T. variegata* as "a bunch of grapes." Two hundred to 300 spherical capsules are surrounded by a mucoid sticky hull which extends into a

Figure 3. Spawn of larvae of *Sinum cymba*. A. Lateral view of spawn (ip = initial portion). Scale bar = 2 cm. B. Vertical transection of spawn to show "cells" containing embryo capsules (c = capsules; e = embryos in early cleavage; s = septa separating "cells"). Scale bar = 300 μ m. C. Side view of protoconch of recently hatched veliger larva (s = suture, arrow indicates ornamentation by granules arranged in bands). Scale bar = 30 μ m. D. Ventral view of protoconch of recently hatched veliger larva (a = aperture; arrow indicates ornamentation). Scale bar = 30 μ m. E. Frontal view of recently hatched veliger larva (b = mouth, c = cilia, e = eyes, o = operculum, p = foot, pr = protoconch, t = tentacle, v = velar lobes).

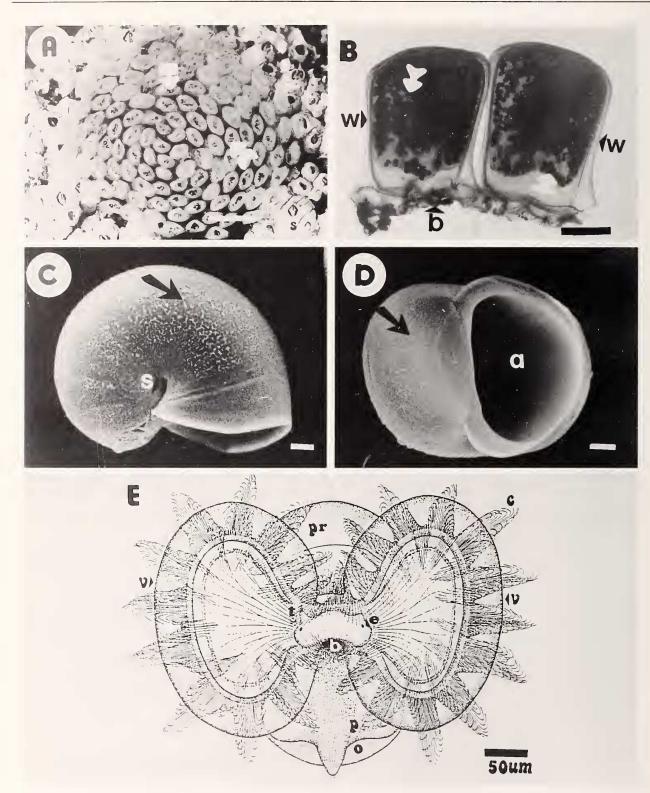


Figure 4. Spawn and larvae of *Priene scabrum*. A. Superficial view of individual spawn adhered to a rocky substrate covered with barnacles (c = capsules; arrow indicates encapsulated embryos; s = barnacles). Scale bar = 1.3 cm. B. Lateral view of capsules with embryos inside. (w = capsular walls, b = basal attachment of capsule, arrow indicates some encapsulated embryos). Scale bar = 2 mm. C. Side view of recently hatched veliger larva (s = initial suture, arrow indicates relief on surface of protoconch). Scale bar = 25 μ m. D. Ventral view of protoconch of recently hatched veliger larva (a = aperture, arrow indicates relief). Scale bar = 30 μ m. E. Frontal view of recently hatched veliger larva (b = mouth, c = cilia, o = operculum, e = eyes, p = foot, pr = protoconch, t = tentacle, v = vclar lobes).

trunklike protrusion, and, by means of it, fuses with other protrusions (Bandel 1976). In comparison with the previously cited species, *T. cingulata* showed a less structured system of organization, with capsules simply enclosed in a gelatinous matrix. Adherence to the substrate was eventually accomplished if the sticky mass became attached soon after spawning. Otherwise it acquired a load of detrital particles, which did not allow the adherence to fixed structures on the bottom. The apparently unprotected nature of this material may be overcome by its camouflage with benthic detritus, as noted by the difficulty of detecting it in shallow water frequently visited by divers.

There is scarce information on reproductive aspects of capsules, eggs, and larval sizes in Turritella species. Nevertheless, the few values that we have found or deduced from the figures show the same tendency that has been suggested for other gastropodos (Spight, 1975)-the larger the egg size, the longer the intracapsular period. In T. cingulata and T communis (Lebour, 1933; Kennedy & Keegan, 1992), the hatching size of the larvae is also greater. Data reported for T. communis differ between localities. In Plymouth, Lebour (1933) determined a capsule diameter of 0.64 mm, and sizes of egg and larvae of 100 and 160 µm, respectively, whereas for the same species in Killary (Ireland), Kennedy & Keegan (1992) determined a capsule diameter of 1.4 mm, and egg and larval sizes of 139 and 229 µm, respectively. Reports of Bandel (1976) for T. variegata and Allmon et al. (1992) for T. gonostoma are incomplete. Bandel (1976) reported the intracapsular development of T. variegata lasting 16-18 days. The author did not mention the egg and capsule size, but based on figure 6 (page 256) we deduce that the size of egg and capsule are 113 µm and 1.8 mm, respectively. The capsule diameter of T. gonostoma varies between 2-3 mm, and the intracapsular development lasts 14 days (Allmon et al., 1992). Relating the size of the eggs with the duration of intracapsular development, T. cingulata had an extremely short period of intracapsular development (7 days) compared with that observed for T. communis (Lebour, 1933), T. gonostoma (Allmon et al., 1992), and T. variegata (Bandel, 1976) with the exception of the data reported by Kennedy & Keegan (1992). More information is required to relate these reproductive aspects.

Sinum cymba

Egg masses of the Naticidae are characterized by their helical band or ribbon form (Giglioli, 1955; Amio, 1955; Gohar & Eisawy, 1967; Hyman, 1967; Robertson, 1974; Barash & Zenziper, 1980; Riddell, 1995). Several characteristics such as the form of the helical band and the size and arrangement of capsules and embryos inside the masses were used to differentiate species. Giglioli (1955) gave a detailed and more extensive classification of the egg-ribbons of the Naticidae, according to the characteristics above described. First, he classified the egg-ribbons into two divisions according to their rigidity or flexibility (I or II, respectively). Then he differentiated subdivisions according to the aspect of the basal margin (smooth, A or plicate, B) and finally, he distinguished according to the size of the capsules (visible to naked eye, a, or not visible to naked eye, b) and embryo arrangements (A to E, layer order of capsules). According to this classification, the eggs of *Sinum cymba* belong to group II, that is flexible wall; A, basal margin smooth; b, capsules not visible to naked eye; and E, capsules grouped.

Amio (1955) added other characteristics such as the manner of connection between the egg capsule and the jelly-wall forming the egg space (egg capsule separable or not separable from the surrounding jelly-wall) and larval morphology. Based on these classifications, the egg masses of *S. cymba* show a close similarity to *Polinices lewisi* Gould, collar C (undetermined egg masses from Iran) (Giglioli, 1955), *Natica adamsiana*, and *N. janthostomoides* (Amio, 1955).

Only the work of Amio (1955) permits some intragenus comparisons. Amio (1955) described the egg masses of Sinum papilla (Gmelin) and six species of Naticidae, including species of Natica and Neverita. Unlike S. cymba, S. papilla presents a plicated basal margin and, in vertical transsection, the capsules are irregularly dispersed on more than one plane, and contain two or three eggs. Furthermore, the larval protoconch of S. papilla is ornamented with spiral lines, and its foot presents a longer metapodial projection that is not observed in S. cymba or in other Naticidae. From the previous comparisons we deduce that beyond the "egg masses like collar" of the family Naticidae, a pattern is not observed which relates the different characteristics from egg masses and the larvae within a genus. Rather, each species presents its own particular characteristics.

Priene scabrum

The egg masses of this species are characterized by the yellow color of the embryos, common in the gastropods Cymatiidae, as well as by the transparency of the capsules. Both characteristics allowed observation of the intracapsular development of the embryos without damaging the capsules, making this material suitable for studies of embryonic development such as the influence of temperature, salinity, effects of toxic materials, and other environmental variables.

There are few descriptions about reproduction in the family Cymatiidae. Available comparisons were those concerning some members of Cymatiidae and the superfamily Tonnacea. Penchaszadeh & De Mahieu (1975) described spawning and development of *Cymatium felipponei* (Ihering, 1907) and *Fusitriton cancellatus* (Lamarck, 1816). These species are similar to *P. scabrum*,

particularly F. cancellatus. Their capsules are vasiform and about 100 capsules are grouped in circular arrangements. These similarities extend to the size, color of eggs, and the indirect development. D'Asaro (1969) described spawning and development of Bursa corrugata Perry, and Distorsio clathrata Lamarck. Bursa corrugata produces egg masses strikingly similar to those of P. scabrum, with regard to the order, form, and size of the capsules. Also the eggs had indirect development and a similar, although smaller larva (175 μ m in length). The egg masses of D. clathrata have a different shape and size compared with P. scabrum. In that species, capsules are lenticular in form and 1.1 mm in diameter with few embryos inside (D'Asaro, 1969). Excepting Distorsio clathrata, the reproductive aspects mentioned here are characteristic of the Tonnacea. Particularly interesting is the fact that all of them have small eggs and larvae and indirect development. Scheltema (1971, 1984) determined that the planktonic larvae of Cymatium nicobaricum (Röding), Cymatium parthenopeum (von Salis), and Charonia variegata (Lamarck) display amphi-Atlantic distribution due to transoceanic migration of planktonic larvae. These larvae belong to the teleplanic larvae group, so named by Scheltema (1971), and they are mainly characterized by a very long planktonic period. The observations on reproduction of Priene scabrum presented in this work will permit study at extracapsular development to determine how the planktonic stage might explain its geographical distribution.

On the other hand, there exists some discord among authors about the taxonomic identity of this species, particularly in genus and species denominations (Marincovich, 1973; Guzmán et. al., 1998; Ramírez, 1987). There is a question as to whether *P. scabrum* and *P. rude* are the same species with variations in shell form (Alan Beu, personal communication). The characterization of the reproductive aspects of *P. scabrum* presented in this work hopefully will contribute to clarifying some of the taxonomic ambiguities in this species.

Finally, the morphology of the larval protoconch is a specific character which may be used to differentiate among larvae collected at sea (Robertson, 1971; Thiriot-Quievréux, 1980). The larvae from the present study, which hatched from laboratory-held capsules, demonstrated similar grades of development and were characteristic of species which have a relatively long planktonic development (Robertson, 1974). Although we have presently described only a few attributes of the embryonic protoconchs of the three species, the size and ornamentation of these provide sufficient information to differentiate between recently hatched larvae.

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